Late-surviving megafauna in Tasmania, Australia, implicate human involvement in their extinction

Chris S. M. Turney[a,b,c], Timothy F. Flannery[c,d], Richard G. Roberts[a,c], Craig Reid[e], L. Keith Fifield[f], Tom F. G. Higham[g], Zenobia Jacobs[a], Noel Kemp[h], Eric A. Colhoun[i], Robert M. Kalin[j], and Neil Ogle[k]

[a]GeoQuEST Research Centre, School of Earth and Environmental Sciences, University of Wollongong, Wollongong NSW 2522, Australia; [d]Division of Environmental and Life Sciences, Macquarie University, North Ryde NSW 2109, Australia; [e]Queen Victoria Museum and Art Gallery, Launceston, Tasmania 7250, Australia; [f]Research School of Physical Sciences and Engineering, Australian National University, Canberra ACT 0200, Australia; [g]Oxford Radiocarbon Accelerator Unit, Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford OX1 3QY, United Kingdom; [h]Tasmanian Museum and Art Gallery, Hobart, Tasmania 7001, Australia; [i]School of Environmental and Life Sciences, University of Newcastle, Newcastle NSW 2308, Australia; [j]David Livingstone Center for Sustainability, Graham Hills Building, University of Strathclyde, Glasgow G1 1XN, Scotland; and [k]Environmental Engineering Research Centre, School of Planning, Architecture and Civil Engineering, Queen's University, Belfast BT9 5AG, United Kingdom

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Establishing the cause of past extinctions is critical if we are to understand better what might trigger future occurrences and how to prevent them. The mechanisms of continental late Pleistocene megafaunal extinction, however, are still fiercely contested. Potential factors contributing to their demise include climatic change, human impact, or some combination. On the Australian mainland, 90% of the megafauna became extinct by ≈46 thousand years (ka) ago, soon after the first archaeological evidence for human colonization of the continent. Yet, on the neighboring island of Tasmania (which was connected to the mainland when sea levels were lower), megafaunal extinction appears to have taken place before the initial human arrival between 43 and 40 ka, which would seem to exonerate people as a contributing factor in the extirpation of the island megafauna. Age estimates for the last megafauna, however, are poorly constrained. Here, we show, by direct dating of fossil remains and their associated sediments, that some Tasmanian megafauna survived until at least 41 ka (i.e., after their extinction on the Australian mainland) and thus overlapped with humans. Furthermore, a vegetation record for Tasmania spanning the last 130 ka shows that no significant regional climatic or environmental change occurred between 43 and 37 ka, when a land bridge existed between Tasmania and the mainland. Our results are consistent with a model of human-induced extinction for the Tasmanian megafauna, most probably driven by hunting, and they reaffirm the value of islands adjacent to continental landmasses as tests of competing hypotheses for late Quaternary megafaunal extinctions.

Paleoclimate | Pleistocene | sea level change | island colonization | human hunting

Since Charles Darwin's discovery of giant ground sloth remains in South America, debate about the cause of global late Quaternary extinctions of megafauna (animals >40 kg) has been intense (1, 2). Potential mechanisms invoked for megafauna demise include climatic change, human and extraterrestrial impacts, or some combination. In Australia, initial human colonization of the mainland occurred by 50 ka[l] (3–5) and has been linked to vegetation reorganization (6) and increased burning (7) in the landscape, driving the megafauna to extinction on the mainland by 46 ka (6, 8, 9). Some workers have argued that most megafauna were extinct before human arrival, citing the apparent disappearance of megafauna in Tasmania before people reached this island as support for extinction driven by climatic and/or environmental change (10, 11).

Currently an island of 68,300 km^2, Tasmania lies 240 km from the mainland across Bass Strait (Fig. 1) with a climate dominated by cyclonic activity associated with prevailing westerly airflow. During the Pleistocene, Tasmania was periodically connected to mainland Australia (12), allowing faunal migrations. The island was isolated for much of the interval 135–43 ka and continuously from 14 ka to the present day, with the first sustained land bridge of the last glacial cycle occurring between 43 and 37 ka (12). Compared with mainland occupation, human colonization was relatively late, with the earliest radiocarbon (^{14}C) ages for arrival being obtained from rock shelters in southwest Tasmania: these indicate a human presence before the oldest radiocarbon-dated horizon of 34,790 ± 510 BP at Warreen Cave (13) (Fig. 1), equivalent to a calendar age of ≈40 ka (14); stone artifacts were present in deeper deposits (13), suggesting that humans arrived in Tasmania between 43 ka (when the land bridge first emerged) and 40 ka.

The Tasmanian megafauna consists of seven species (six marsupials and one monotreme), which also occurred on mainland Australia. There is some evidence of subspecific endemism: Tasmanian S*imosthenurus occidentalis* have different dental proportions from those of the adjacent mainland (15), and Tasmanian *Thylacoleo* also exhibit distinctive dental features.

The island has yielded abundant remains, with at least eight locations in the northwest and south, producing thousands of bones (16, 17) (see Table 1). No Tasmanian megafaunal remains have hitherto been reliably dated. Early attempts at dating suggested that megafauna may have survived until relatively recently. For example, charcoal associated with megafaunal remains in Titans Shelter (17) was radiocarbon dated to 14,310 $^{+2,970}/_{-2,160}$ BP. Subsequent direct dating of bone from this site by using amino acid racemization (AAR) and electron spin resonance (ESR) gave ages of 40–27 ka, suggesting that the dated charcoal was intrusive (18). No megafaunal remains have been found in human occupation sites (19), but only 0.6% of the material examined dates to the first 4 ka of human occupation, so any temporal overlap of humans and megafauna may have been missed (20).

Results and Discussion

We undertook dating and paleontological investigations of archived fossil material from four reported megafauna sites in

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[b]To whom correspondence should be sent at the present address: School of Geography, Archaeology and Earth Resources, Department of Geography, University of Exeter, Exeter, EX4 4RJ, United Kingdom. E-mail: c.turney@exeter.ac.uk.

[c]C.S.M.T., T.F.F., and R.G.R. contributed equally to this work.

[l]In this paper, calibrated radiocarbon ages and those derived from alternative dating methods are reported as ka (thousands of calendar years ago). Uncalibrated radiocarbon ages are reported as BP (before present; relative to 1950 AD).

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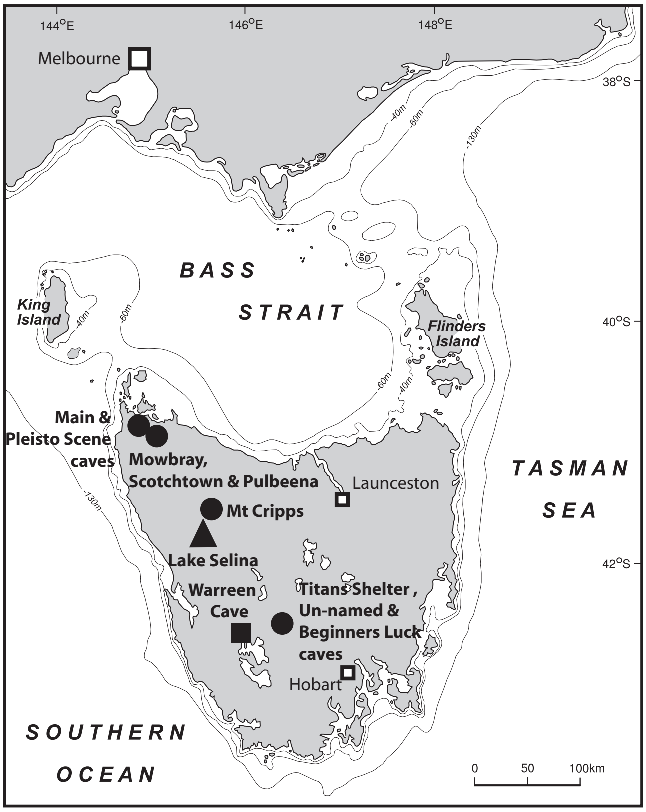

Fig. 1. Locations of megafaunal, environmental, and archaeological sites in Tasmania. Megafaunal sites are marked with solid circles, Lake Selina with a closed triangle, and Warreen Cave with a solid square.

Tasmania [Fig. 1 and supporting information (SI) Tables S1–S3]: Pleisto Scene Cave, Scotchtown, Titans Shelter, and Un-named Cave. In addition, new fossil finds were investigated from Mount Cripps (chambers CP118 and CP213). To avoid concerns about intrusive charcoal and other associated carbon (18), we applied ^{14}C dating to bone collagen, by using either demineralization followed by gelatin extraction and step-combustion (C-SC) or gelatin isolation with ultrafiltration (C-AF) (21). The ^{14}C content was measured by accelerator mass spectrometry, and the ages were calibrated following ref. 14. The fossiliferous cave sediments were dated by optically stimulated luminescence (OSL), which indicates the time elapsed since the sediment grains were last exposed to sunlight (22). In sequences with articulated megafaunal remains in primary context, OSL dating gives the time of fossil burial; where no articulation is observed, minimum estimates of burial age are obtained. Full ^{14}C and OSL dating details are given in *SI Dating Methods and Results*.

The Tasmanian megafauna dated in this work provide a record encompassing much of the late Pleistocene, from >127 to 41 ka (see Table 1 and Tables S1–S3). The deposits in Pleisto Scene Cave contained skeletal elements of megafauna in articulation and were dated by OSL to marine isotope stage (MIS) 5e or earlier (>120 and >127 ka, the infinite ages arising from dose saturation of these samples). The Un-named Cave deposits gave an OSL age of 103 ± 9 ka, which is indistinguishable from the 97-ka age obtained on the nonarticulated remains with ESR (18). Evidence of articulation was also not reported for the rich megafaunal site of Scotchtown Cave, which was interpreted as a carnivore lair (16). Because articulated remains are not expected in such contexts, it is not unreasonable to assume that the OSL age of 56 ± 4 ka, obtained for sediment grains in a mixed soil–bone sample from the original excavation, approximates that of the entombed fauna. The samples from all of these sites had negligible collagen content and were unsuitable for ^{14}C dating.

Younger ages for Tasmanian megafauna were obtained from Titans Shelter and Mount Cripps. A *Protemnodon anak* specimen was obtained from Titans Shelter and dated by ^{14}C (C-SC) to 39,980 ± 610 BP, equivalent to ≈44 ka (Table S1). At Mount Cripps (chamber CP213), faunal remains were discovered lying on the chamber floor and wedged in rock crevices; their state of preservation was excellent. An entire cranium was recovered and most of

Table 1. Ages and faunal assemblages of principal Tasmanian megafaunal sites

Event	Age of unit(s), ka	*Megalibgwilia* sp.	*Thylacoleo* sp.	*Palorchestes azael*	*Zygomaturus trilobus*	*Protemnodon anak*	*Simosthenurus occidentalis*	*Metasthenurus newtonae*
Human arrival in Tasmania	43–40							
Mount Cripps, CP213	42.9–40.9					X		
Mount Cripps, CP118								X
Titans Shelter, Site G	44				?	X	X	
Mowbray Swamp	>38				X			
Main Cave (MU201)							X	
Pulbeena Limeworks	>54			X				
Scotchtown Cave	56 ± 4	X	X	X	X	X	X	X
Beginner's Luck Cave M (JF-79)	80–63		X				X	
Un-named Cave (JF-155)	103 ± 9		X			X	X	
Pleisto Scene Cave B (MU203–205; 206)	>127 ± 28 >120 ± 21	X	X	X	?	X	X	

See *Supporting Information* for further details. Note that human arrival in Tasmania is contemporaneous with the most recently dated megafaunal remains from Mount Cripps, demonstrating that there was some overlap (albeit brief) between humans and megafauna. That the megafauna had survived on Tasmania for millions of years prior to human arrival suggests that the sudden disappearance of megafauna was caused by humans.

GEOLOGY

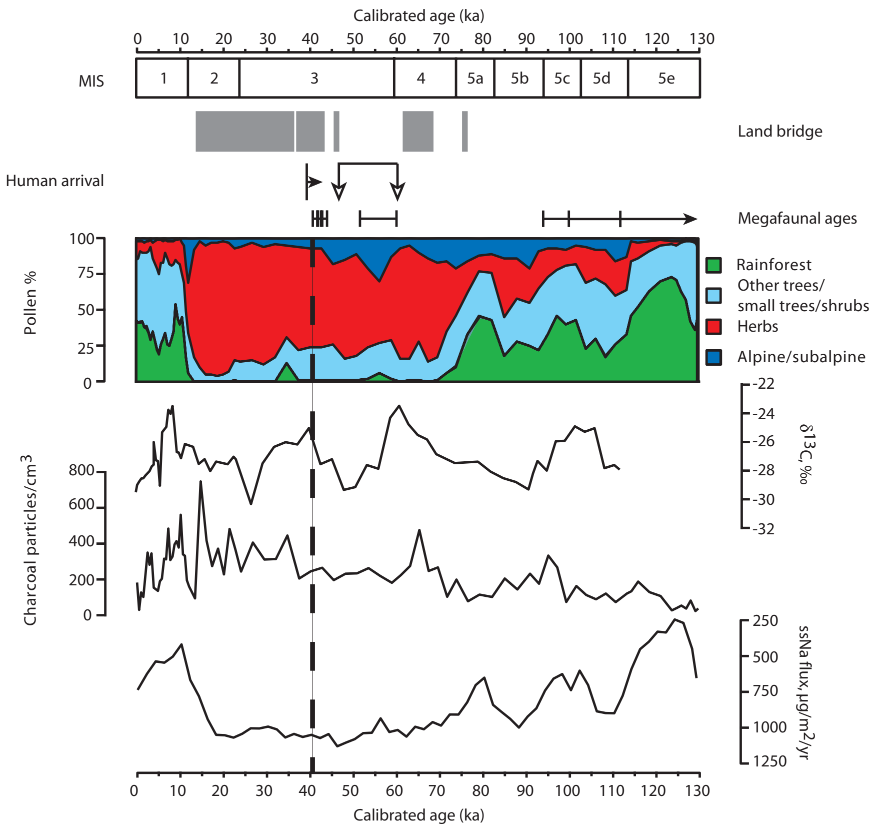

Fig. 2. Environmental and climatic changes in Tasmania and the Southern Ocean. Solid gray boxes denote when a land bridge was established between the Australian mainland and Tasmania (12). For human arrival, solid (black) arrow indicates minimum age for earliest known occupation of Tasmania (13); open (white) arrows delimit 1 SD age range for earliest occupation of mainland Australia (3–5). Ages associated with megafaunal remains dated in this work are shown as 1 SD ranges. Dashed line denotes (minimum) overlap between most recent megafaunal remains and earliest human arrival in Tasmania. Summary plots of vegetation change (26), charcoal concentration (26), and $\delta^{13}C$ of bulk sediments (this work) are from Lake Selina. Sea-salt sodium (ssNa) flux is a measure of winter sea-ice cover in the Southern Ocean, as recorded in the EPICA ice core (28); note that the ssNa flux scale is inverted.

a second specimen. No skeletons were articulated, but associated elements were found in close proximity. The only megafaunal species present in the deposit was *P. anak*, of which the remains of three individuals are represented: a large subadult (QVM:2001:GFV 5, body mass estimate ≈60 kg) (23), a pouch young (QVM:2001:GFV 9), and a young at foot (QVM:2000:GFV 10, body mass estimate ≈30 kg) (see Tables S4 and S5). OSL dating of sediment wedged in the nasal cavity of the subadult yielded an age of 36 ± 3 ka (Table S3 and Fig. S1), which we view as a minimum age for the skull because the sediment grains were emplaced postmortem. Radiocarbon dating of two individuals from Mount Cripps, with C-SC pretreatment, produced ages of 32,780 ± 370 BP and 30,400 ± 270 BP, but significantly older ages of 36,200 ± 300 BP and 37,920 ± 340 BP were obtained from duplicate samples by using the C-AF procedure (Table S1); the latter is thought to yield more accurate ages for ancient bone (21). We attribute the younger C-SC ^{14}C ages to the incomplete removal of low-molecular weight contaminants from the gelatin. The C-AF ^{14}C ages are therefore considered more reliable. When these ages are calibrated and considered in conjunction with the OSL age from Mount Cripps, they indicate that Tasmanian megafauna survived to at least 42.9–40.9 ka (at 1 SD).

The Scotchtown and Pleisto Scene Cave deposits differ in age by >70 ka (from ≈56 to >127 ka) but contain essentially the same suite of megafauna (Table S4), the only exception being *Metasthenurus newtonae*, which is represented by three isolated molars at Scotchtown (and known also from an undated context at Mount Cripps, chamber CP118). If our assumption is correct that the OSL age of the sediments at Scotchtown approximates that of the faunal remains, then Tasmania experienced no significant change in its faunal diversity between the last interglacial (MIS 5e) and the succeeding glacial stages. The survival of all seven species of Tasmanian megafauna until at least 56 ka argues against proposals for a staggered series of climate-induced extinctions before human arrival (10), similar to findings on the Australian mainland (9, 20, 24, 25).

As an independent test of possible climatic and/or environmental influences (including anthropogenic burning) on megafaunal extinction (6, 10), we investigated the late Quaternary vegetation and charcoal records preserved in Lake Selina (Fig. 1), which provides a crucial southern midlatitude perspective on paleoecological changes over the past 130 ka (26). The pollen record indicates that cool temperate rainforest was present during MIS 5e and the Holocene (MIS 1), with grassland, herbs, and heath vegetation dominating throughout the intervening period (Fig. 2). There is no evidence of a significant increase in burning at the time of human arrival or any associated shift in vegetation. The bulk sediments exhibit a relatively narrow range of stable carbon isotope values ($\delta^{13}C$), reflecting the local C_3 vegetation, with the small fluctuations probably representing changes in lake productivity. No major change occurred at 41 ka.

The overall vegetation trend at Lake Selina mirrors other regional proxies of environmental and climatic conditions (27), including winter sea-ice cover in the Southern Ocean, as inferred from the sea-salt sodium flux in Antarctica (28) (Fig. 2). Elevated levels of sea-ice persisted from ≈65 to 17 ka, with no significant deviation at 41 ka. Furthermore, we note that moa extinction did not take place "downwind" in New Zealand at this time (29). We consider it highly unlikely, therefore, that climatic or environmental change could have played a significant role in the demise of the megafauna on Tasmania.

Although our dataset is small, the results show that megafauna persisted in Tasmania until at least 41 ka, which is similar to, or slightly later than, the time of extinction on the Australian mainland (48.9–43.6 ka at 1 SD) (9, 30). Importantly, the 41-ka age postdates the establishment of a land bridge across the Bass Strait and is statistically concordant (χ^2 test $T = 3.39$; $5\% = 3.84$) with the minimum age for the earliest evidence of humans in

Tasmania [Warreen Cave (13)]. This introduces the possibility, hitherto discounted (10, 11), that humans caused the extinction of the Tasmanian megafauna. Because we find no evidence for a major change in vegetation and/or fire dynamics [in contrast to the mainland (6, 7)] and because the megafauna had relatively low reproductive rates, we favor the hypothesis that human hunting led to a rapid population collapse (31). A brief coexistence of humans and megafauna is consistent with the absence of megafaunal remains at human occupation sites (19). To elucidate the precise mechanism of extinction will require improved age estimates for both the first human arrivals and the last-surviving megafauna in Tasmania.

Materials and Methods

Samples for ^{14}C dating were obtained from museum specimens held in collections at Launceston and Hobart. Fragments of bone were hand-picked, and the collagen was extracted in two ways. At the University of Wollongong (C-SC pretreatment), bone fragments were washed in distilled water to remove surface contaminants, then they were broken into small pieces and decalcified with dilute hydrochloric acid. The gelatin was isolated and step-combusted to remove any labile contaminants. The CO_2 evolved at 850°C was collected, purified, and graphitized for accelerator mass spectrometry (AMS) radiocarbon measurement at the Australian National University (ANU). At the University of Oxford (C-AF pretreatment), coarsely ground bone powder was given a series of acid, base, and acid washes, rinsing with ultrapure water between each reagent. Crude collagen was gelatinized, and the >30-kDa gelatin fraction was isolated by ultrafiltration for AMS radiocarbon measurement at Oxford (21). All ^{14}C ages were calibrated following ref. 14. For stable isotope analysis, samples were combusted in an elemental analyzer interfaced to a continuous-flow isotope-ratio mass spectrometer at ANU (extracted gelatin) and Queen's University Belfast (Lake Selina). Bulk sediments from Lake Selina were treated before measurement with dilute hydrochloric acid to remove carbonates, and the CO_2 evolved was analyzed for isotopic abundance by gas chromatography. $\delta^{13}C$ values are reported as per mille (‰) relative to the PDB scale; analytical precision is $\pm$ 0.15 ‰ at 1 SD. Sediment samples for OSL dating were obtained from the Launceston and Hobart museum collections, and analyzed at the University of Wollongong. Quartz grains of 90- to 250-μm diameter were extracted from the light-safe portion of each sample and purified by using standard procedures, including etching with hydrofluoric acid to remove the external α-dosed layer. The burial ages were calculated from the equivalent dose, estimated by using a single-aliquot regenerative-dose procedure (22), divided by the total dose rate arising from ionizing radiation.

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